Perplexing siskins: a review of the *Spinus pinus–S. atriceps* problem

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Summary.—Black-capped Siskin *Spinus atriceps* and the southernmost form of Pine Siskin *S. pinus perplexus* have long been confused. We outline the taxonomic history of the complex and present a review of morphological characters based on the largest series yet assembled. Olive-morph birds are morphologically distinctive and are correctly associated with the name *atriceps*, although Salvin's original description also included a grey-morph specimen.

The highlands of southern Mexico and Guatemala (Fig. 1) form an area of endemism for birds (Peterson *et al.* 1998, Stattersfield *et al.* 1998, Watson & Peterson 1999), and two taxa of *Spinus* are confined to this region—Black-capped Siskin *Spinus atriceps* (Salvin, 1863) and Pine Siskin *S. pinus perplexus* van Rossem, 1938. Three plumage morphs have been variously associated with the two names: birds that are mainly olive, those that are mainly grey, and birds that are streaked brown and white (Fig. 2). Uncertainty concerning nomenclature and species limits in this complex has persisted for 150 years. Plumage variation in *S. atriceps* is poorly understood, and siskins from southern Mexico and Guatemala with mostly or partially grey plumage have sometimes (AOU 1983, Sibley & Monroe 1990) been regarded as hybrids with *Spinus pinus* (Wilson, 1810), following van Rossem (1938). We outline the taxonomic history of the complex and present a review of morphological characters in the available material of *S. atriceps* and *S. pinus*.

Taxonomy and nomenclature of *Spinus atriceps*

O. Salvin described *Chrysomitris atriceps* (1863) from two specimens taken in August 1862 by R. Owen and himself in the highlands of western Guatemala near Quetzaltenango, dpto. Quetzaltenango, at an elevation of 8000 feet (14°50'40"N, 91°30'05"W; 2,440 m). Both possess a distinctive black crown. Although both are adult males, they otherwise differ strikingly in plumage. One (Natural History Museum, Tring, BMNH 1885.12.14.1179, Fig. 3a) is mostly olive-plumaged, the other (BMNH 1885.12.14.1180, Fig. 3b) is similarly patterned (including the blackish crown), but has a mostly grey head, underparts and mantle. The breast has some scattered olive feathers. Salvin's description begins: *'Olivacea; capitis lateribus griseis; abdomine medialiter cinereo; dorso postico et uropygio viridescenti-flavis; pileo toto et gula nigris, hac obscuriore…'*, which we translate thus: 'Olivaceous; with sides of head grey; middle of belly ash-grey; back and rump are green-yellow; whole cap and throat black, of which [the throat is] darker…'. These characters match the grey and not the olive bird. Salvin (1863) added 'The *two specimens* from which the above description was taken differ considerably in colouration from one another, one being in old and somewhat worn plumage, the *other* more freshly moulted and brighter *olivaceous*' (our emphasis). In the *Biologia Centrali-Americana*, Salvin & Godman (1886: 429–430, for dating see Dickinson *et al.* 2011) repeated Salvin's Latin description, which they noted applied only to the grey specimen, whereas 'the *other* specimen is of a much more olive-colour above and below, this taking the place of the grey colouring of the under surface' (our emphasis). A colour plate illustrated the syntypes (Fig. 4). Thus, although Salvin (1863) did not designate a holotype

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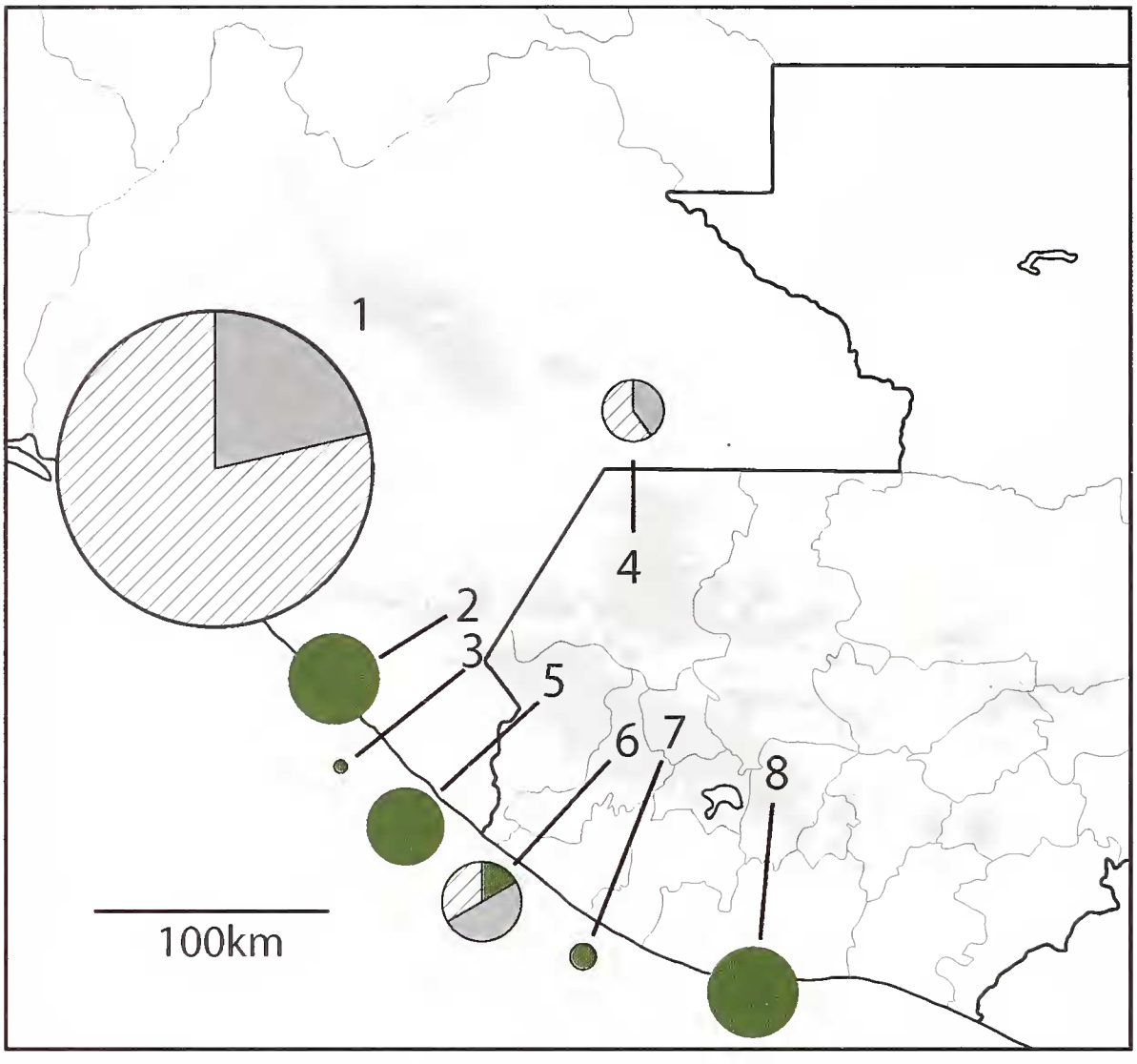

Figure 1. Map of southern Mexico (sites 1–3) and western Guatemala (4–8) showing collecting localities and distributions of three morphotypes in the *Spinus atriceps / pinus perplexus* complex. Shaded areas = >2,000 m in elevation. Pie charts show distributions and co-occurrence of morphotypes; striped = streaked morph, grey = grey morph and olive = olive morph. Sizes of individual pie charts proportional to sample sizes at each site (1) San Cristóbal area, n = 28; (2) southern highlands of Chiapas, n = 7; (3) Tacana, Chiapas, n = 1; (4) Chancol, dpto. Huehuetenango, n = 5; (5) San Marcos, dpto. San Marcos, n = 6; (6) Quetzaltenango, dpto. Quetzaltenango, n = 6; (7) Desconsuelo, dpto. Totonicapán, n = 2; (8) Tecpán, Chimaltenango, n = 7.

in present-day fashion (the two specimens are syntypes), he chose the grey-plumaged bird for his diagnosis, presumably because he believed it to be more fully adult.

Ridgway (1884) reached the opposite conclusion in determining the age of these specimens. He examined the syntypes of *C. atriceps* and noted the variable colour of the underparts describing them as 'yellowish olive (in some specimens dull greyish).' Later, in his account for *S. atriceps* in *The birds of North and Middle America* (Ridgway 1901), he compared them with two additional specimens in the United States National Museum, Washington DC. Presumably, these are the birds taken on 9 January 1896 at Hacienda Chancol, dpto. Huehuetenango, Guatemala (USNM 143725) and 24 September 1895, at San Cristóbal, Chiapas, Mexico (USNM 143724). Ridgway determined the olive syntype to be an adult male and tentatively regarded the grey syntype as an 'immature male (?)' He considered one of the birds (USNM 143725), also grey, to be an 'immature (?) male' of *C. atriceps* and an unsexed bird (USNM 143724) to be an 'immature (?) male' *C. atriceps*.

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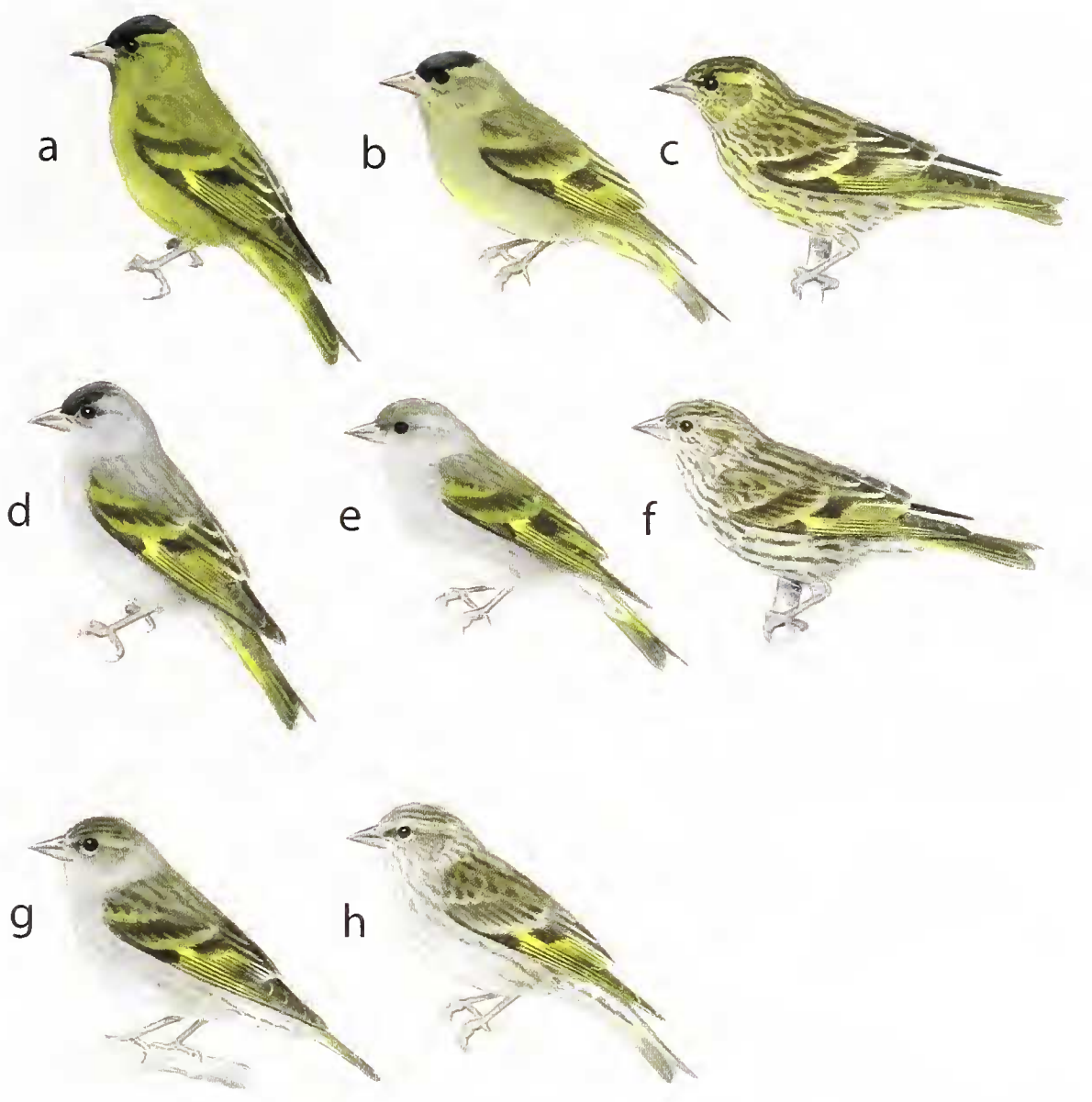

Figure 2. Plumage morphotypes in the *Spinus atriceps / pinus perplexus* complex: (a) olive morph typical adult male, (b) olive morph typical adult female, (c) olive morph juvenile, (d) grey morph typical adult male, (e) grey morph typical adult female, (f) unknown juvenile, (g) streaked morph adult, greyish extreme, (h) typical streaked morph adult (Dale Dyer)

Taxonomy and nomenclature of *Spinus pinus perplexus*

In 1933 and 1938, A. J. van Rossem examined material in the British Museum (Natural History) (BMNH), with the aim of identifying and segregating types of American birds, during which work he described no fewer than 21 new subspecies of birds from Mexico and Guatemala (van Rossem 1938, see Miller 1957, Warren 1966: iv), among them *S. pinus perplexus*. For the type, van Rossem designated a brownish, streaked, adult female (BMNH 1899.2.1.2116) collected by W. B. Richardson at San Andrés, Chiapas, Mexico (16°53′01″N, 92°42′48″W) on 11 May 1897. His description reads: 'Differs from *Spinus pinus pinus* (Wilson) of North America and *Spinus pinus macropterus* (Du Bus) of Mexico in more slaty (less brownish) and slightly darker dorsal coloration and more obsoletely streaked underparts; size slightly smaller than *S. p. pinus* and decidedly smaller than *S. p.*

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macropterus.' The holotype (Fig. 3c) is similar to many northern specimens of *S. pinus* but is generally greyer, with the streaking on the underparts and mantle somewhat less distinct and less contrasting.

By the time of van Rossem's visits, the BMNH series included Salvin's types of *S. atriceps* and an additional 18 specimens collected by W. B. Richardson in 1890 and 1897, in the highlands of southern Mexico (Chiapas) and western Guatemala. The Richardson material includes siskins with a range of plumage characters including mostly olive specimens with black caps and yellow bellies (Fig. 2a), mostly grey birds with blackish caps and white bellies (Fig. 2d), mostly grey birds with concolorous grey caps, and streaked brown-and-white birds that resemble northern examples of widespread *S. pinus* (Fig. 2g–h). Van Rossem regarded the mostly olive, black-capped plumage (including the olive syntype of *C. atriceps*, BMNH 1885.12.14.1179) as adults of *S. atriceps*, but the grey-plumaged birds (including Salvin's grey syntype) as 'intermixtures' with *S. pinus*. His description lists six specimens as *S. p. perplexus*, and seven grey birds as 'intermixtures' between *S. pinus perplexus* and *S. atriceps*. Van Rossem (1938) stressed the significance of bill morphology as a diagnostic character, noting that the bill of *S. atriceps* is longer and more slender than that of *S. p. perplexus*, and remarking 'were it not for the very differently shaped bills it might be argued that one dimorphic species was present.' He added that 'these species give every evidence of undergoing complete amalgamation.' In a cryptic remark he hinted that 'the situation ... is too involved to be discussed here in full', but he did not revisit the issue subsequently.

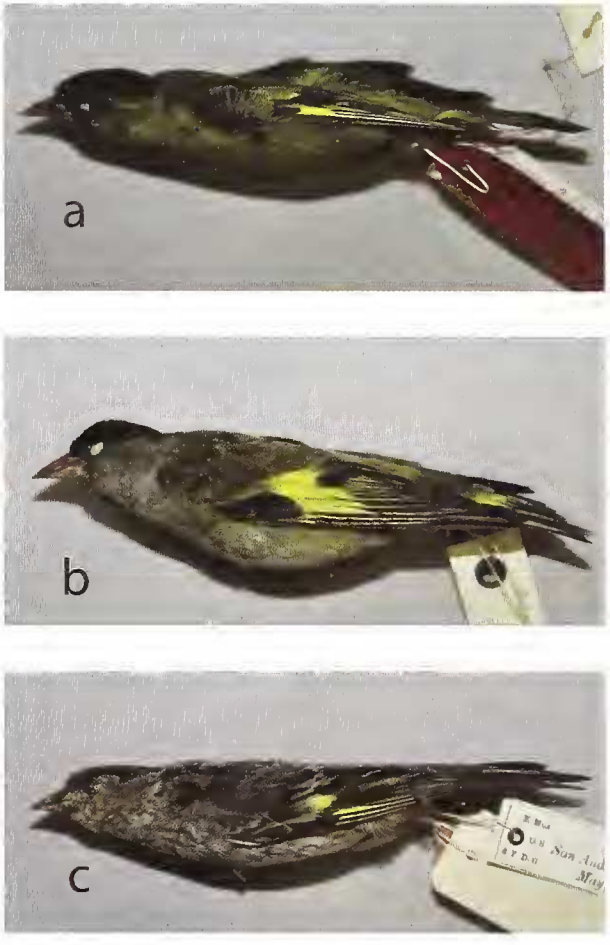

Figure 3. Type specimens in the *Spinus atriceps* / *pinus perplexus* complex: (a) olive syntype of *Spinus atriceps* (Salvin, 1863), BMNH 1885.12.14.1179, (b) grey syntype of *Spinus atriceps* (Salvin, 1863), BMNH 1885.12.14.1180, (c) holotype of *Spinus pinus perplexus* van Rossem, 1938, BMNH 1899.2.1.2116 (Tom Trombone / © Natural History Museum, London)

Confusion surrounding the taxonomy of the grey birds is reflected in the Nelson & Goldman series (USNM 143723–725) being relabeled *Carduelis pinus perplexa* by P. Brodkorb, in newly collected grey birds determined as *S. p. perplexus* by R. T. Moore (Moore Zoological Laboratory, MZL 57023), two specimens identified as '*atriceps*' by A. R. Phillips (Delaware Museum, DMNH 34695, 34696), and a specimen with the label annotated 'hybrid' in the Louisiana State University Museum of Zoology, Baton Rouge (LSUMZ 49577). More recently, Arnaiz-Villena *et al.* (2007, 2008) presented a study of New World *Spinus* siskins based on mtDNA. These included blood samples from single individuals identified as *S. p. perplexus* and *S. atriceps* trapped in dpto. Quetzaltenango, Guatemala. No vouchers were preserved by those workers. Photographs in their publications show a siskin with boldly streaked underparts labeled *S. p. perplexus*, and a grey-plumaged bird with black cap labeled *S. atriceps*.

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Materials and Methods

We searched museum collection databases to compile a database of specimens catalogued either as *S. p. perplexus*, as *S. atriceps*, or as hybrids of *S. pinus* and *S. atriceps* (Appendix 1). We sorted specimens into three morphotypes and examined specimens and photographs for indications of plumage wear and moult to determine age (juvenile or adult). Where possible we obtained measurements of bill depth, bill length (nostrils to tip) and wing chord. We excluded immatures and birds in primary moult from our morphometric analysis. We used principal component analysis (PCA) to reduce the dimensionality and complexity of the morphometric data. A PCA based on the correlation matrix of three traits (bill length, bill depth and wing chord) was used to derive allometric size and shape variables (*cf.* Perktaş & Gosler 2010, Perktaş 2011). PCA derived three principal components. Because PC1 explained most of the variance among individuals (Table 1), we used individual PC1 scores for further statistical analyses. Before analysing individual PC1 scores, we tested normality and homogeneity of variances using the Kolmogorov-Smirnov test ($Z = 0.524$, $p > 0.05$) and Levene statistics ($Levene\ statistic_{2, 26} = 0.471$, $p > 0.05$) respectively. We then used one-way ANOVA to reflect shape differences among the three morphotypes. Hocberg's GT2 method (for unequal sample sizes, Quinn & Keough 2002) was used for multiple comparisons.

Results

We located 74 specimens from Chiapas, Mexico or Guatemala that have been catalogued as *S. p. perplexus*, as *S. atriceps*, or as hybrid *S. pinus* × *S. atriceps*. We personally examined 45 of these specimens, and reviewed photographs of an additional 21 (Appendix 1). We sorted specimens ($n = 66$) into three morphotypes (Fig. 2). Notations in parentheses following colour names refer to Ridgway (1912).

The primaries, secondaries and rectrices of all three morphotypes are similarly coloured, being mostly blackish brown (21'''m). The outer web of each primary is finely edged yellow (23b) to the emargination. The base of each primary, excepting the outer two or three, are yellow. The bases of the secondaries are also yellow and the secondaries are fringed yellow from the tip to a point short of the yellow basal patch. On the folded wing the yellow bases of the remiges are mostly or completely covered by the wing-coverts and there is a dark band between the panel of yellow fringes on the secondaries and coverts. The rectrices are yellow at the base of the inner web on all but the central feathers. Yellow extends to the outer web at the base of the outermost feathers.

Olive morphotype.—Adults ($n = 19$) are mostly uniform in coloration though some individual variation is evident. All olive-morph adults have a black cap. In most specimens ($n = 11$) the remaining upperparts are dark olive (23''k), except the rump, which is olive (23''). The throat, and in some examples, the fore cheeks, are blackish. Otherwise the face, breast and flanks are olive (23''). The central belly and undertail-coverts are pale yellow (23'b). The undertail-coverts are streaked brown. The wing-coverts are blackish brown (21'''m) basally and broadly tipped yellow-olive (23). Yellow-olive extends over half of the greater coverts and most (or all) of the median and lesser coverts. The tertials are blackish brown fringed laterally with yellow-olive (23) and have whitish tips (Fig. 2a). Some adults ($n = 8$) including most females and one male are an overall greyer shade of olive, and the yellow underparts may be paler. These also lack any black on the throat (Fig. 2b).

Olive-morph juveniles ($n = 2$) are streaked very dark brown (21'''m) and pale brown (21'''b) above, the cap sometimes being almost uniformly dark. The rump may be paler, and more yellow, approaching yellow-olive (23''b). The face, breast and flanks are yellowish

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white with dark brown (21'''k) streaks with a distinctive wedge, or chevron, shape. The wing-coverts and tertials are tipped yellowish white (Fig. 2c). Three specimens (AMNH 30976, WFVZ 14541, 14543) show varying extents of streaked plumage and patches of plain olive, thereby demonstrating the progression between juvenile and adult plumage in this morphotype.

Olive-morph birds are known only from Guatemala and the southern Chiapas highlands. Guatemalan specimens are available from Tecpam [=Tecpán] dpto. Chimaltenango (n = 7), Quetzaltenango, dpto. Quetzaltenango, (n = 1), San Marcos, dpto. San Marcos (n = 6), and Desconsuelo, dpto. Totonicapán (n = 2). Mexican specimens are from Cerro Male, Chiapas (n = 7) and Volcán Tacana, Chiapas (n = 1). This form is unknown from the San Cristóbal region of central Chiapas, Mexico, and we have not seen specimens of this morph from dpto. Huehuetenango, Guatemala (Fig. 1).

Grey morphotype.—Adults (n = 11) are rather uniform except in crown colour, which may correlate to sex. Adult males (n = 9) have a blackish cap that is not as black as in olive birds, and in one example breaks into spots at the rear. Most of the remaining upperparts, including the crown of cap-less birds (n = 2), are dark grey (21''''), with faint browner streaks, sometimes mixed with olive on the lower back. The rump is dusky yellow (23''b; i.e. paler than the olive rump of olive-morph birds). Some males have a faint blackish smudge on the throat. Otherwise the face, breast and flanks are neutral grey (23''''d), sometimes with very faint brownish flanks streaking. The belly and undertail-coverts are white, the latter streaked brown. The wing-coverts are blackish brown basally and broadly tipped yellow-olive (23). Yellow-olive extends over half of the greater coverts and most (or all) of the median and lesser coverts. The tertials are blackish brown fringed laterally with yellow-olive and have whitish tips (Fig. 2d–e). Juvenile plumage is unknown.

Grey morphs have been collected in dpto. Quetzaltenango, Guatemala (n = 3), Chancol, dpto. Huehuetenango, Guatemala (n = 2), and in the San Cristóbal region of central Chiapas, Mexico (n = 6).

Streaked morphotype.—This form includes the holotype and type series of *S. pinus perplexus* and is the most variable morphotype. It is streaked very dark brown (21'''b) and pale brown (21'''m) from crown to lower back. Overall coloration is variable, but is always greyer (less warm or brownish) than other forms of *S. pinus*. Streaked-morph birds are also usually darker overall than in other forms of *S. pinus*, including on the crown. The streaking varies from soft to moderately crisp, but is usually less contrasting and well defined than in other forms of *S. pinus*. The rump varies from pale beige (21'''d / 17'''d) to concolorous with the mantle, or from very pale yellow to dusky yellow, and usually shows some streaking. The face, breast and flanks vary from streaked pale greyish brown (21''''b) and whitish, to broad, soft, brownish-grey streaking with the white markings narrower, yielding a more muted, uniform appearance. The belly and vent are whitish, or yellowish white in two juveniles, and the undertail-coverts are streaked brown. Wing-coverts are narrowly tipped whitish, beige or olive-beige, and may show narrow yellowish lateral fringes to the greater coverts. The tertials are narrowly fringed whitish or yellowish and tipped whitish (Fig. 2g, h). Some streaked birds with juvenile rectrices are similar in plumage to adults.

Streaked-morph birds have been collected at Quetzaltenango (n = 2), Chancol, dpto. Huehuetenango, Guatemala (n = 3) and in the San Cristóbal region of central Chiapas, Mexico (n = 22).

We examined two additional juveniles that we cannot confidently assign to any of the three morphotypes (Fig. 2f). Both are boldly streaked brown below. The wing-coverts in these specimens are tipped cinnamon (17'''b) as in juvenile *S. p. pinus*. Two additional specimens may represent either this plumage or be juveniles of the olive morph (Fig. 2c).

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Figure 4. Illustration of *Spinus atriceps* from Salvin & Godman (1886)

Morphometric analysis

PC1 explained most of the variance among individuals (Table 1). PC1 had relatively high positive factor loading for bill length (nostril to tip), and negative factor loadings for wing length and bill depth. Hence, PC1 was taken to be a measure of bill shape, whereby specimens with higher PC1 scores have a longer and more slender bill and relatively shorter wing length. ANOVA detected a significant difference in PC1 scores among morphotypes ($F_{2, 28} = 10.978$, $p < 0.001$). Multiple comparisons revealed that both sexes of the olive morphotype had longer and more slender bills, and relatively shorter wing length in comparison to both the grey and streaked morphotypes (Fig. 5).

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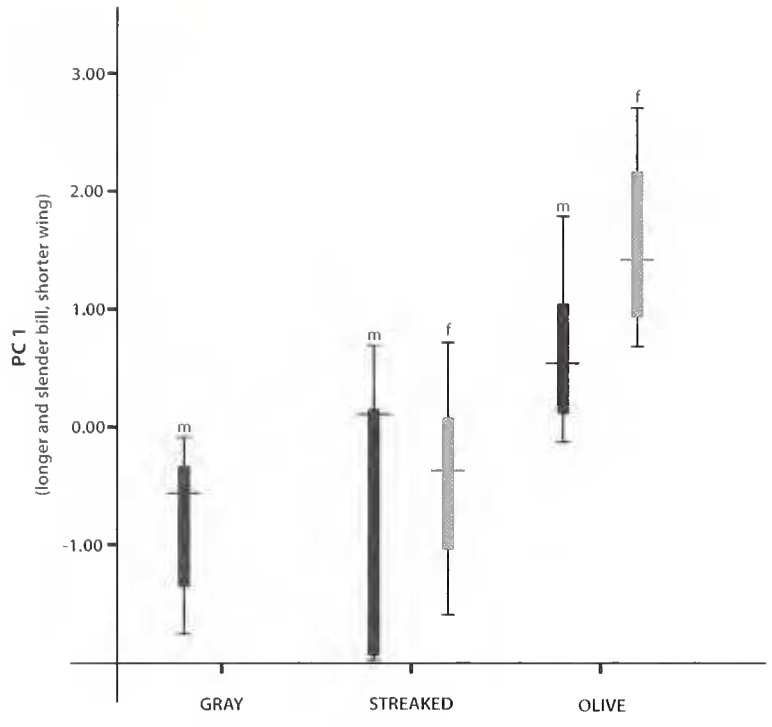

Figure 5. Variation in PC1 among morphotypes in the *Spinus atriceps / S. pinus perplexus* complex. Olive-morph birds differ significantly from grey and streaked morphotypes: mean difference = -1.794, p = 0.003; between streaked and olive morphotypes: mean difference = -1.476, p = 0.001)

Discussion

Plumage maturation and hybridisation have been advanced to explain variation in this complex (Ridgway 1901, Salvin & Godman 1886). Specimens in moult from a streaked juvenile to plain olive plumage (see above) demonstrate, however, that grey plumage does not represent a stage in the olive bird's maturation. While all juvenile siskins that we examined are streaked, many streaked birds have adult-shaped rectrices and some bear labels indicating gonads in breeding condition. Also, all grey-morph birds examined are at least post-juvenile. Plumage maturation is thus eliminated as an explanation for the olive and grey morphs.

Van Rossem's (1938) suggestion that variation in this complex is evidence of hybridisation must be reassessed in light of the larger series assembled for this study. The grey morphotype, including those birds regarded by van Rossem as 'intergrades' or 'intermixtures' are, in colour, unlike either of the supposed parent forms, and do not appear to present an intermediate character state. However, some grey-morph birds possess a limited number of olive feathers, usually on the mantle and sometimes the underparts (i.e. the grey syntype of *S. atriceps*). Grey-morph birds can also exhibit limited faint brownish flanks streaking. Birds of the streaked morph can be clearly streaked brown on white,

TABLE 1
Principal component loadings from analysis of three morphological traits in *Spinus pinus / S. atriceps* specimens (n = 29).

Variables	Factor loadings		
	PC1	PC2	PC3
Wing chord	-0.667	-0.512	0.540
Bill length (nostril to tip)	0.732	0.137	0.668
Bill depth	-0.552	0.801	0.232
Variance explained (%)	42.9	30.8	26.3

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TABLE 2
Summary of morphological characters in the *Spinus pinus perplexus* / *S. atriceps* complex (adults). Measurements (mm) made with dial callipers. Range (mean).

	olive morph	grey morph	streaked morph
cap	black	black in all known males, known females grey streaked brown	streaked light / dark brown
back	dark olive	grey or olive-grey, streaked brown	streaked light / dark brown
rump	yellow-olive	yellowish grey	paler and more softly streaked than back, sometimes yellowish
throat, face	blackish or olive throat, olive face	blackish or grey throat, ash-grey face	softly streaked pale brown or grey-brown on whitish ground colour
breast, flanks	olive	ashy grey	softly streaked pale brown or grey-brown on whitish ground colour
belly, undertail-coverts	yellow, undertail-coverts streaked dark	white, undertail-coverts streaked dark	white, undertail-coverts streaked dark
tertials	blackish, with broad olive or yellowish lateral fringes, whitish tips	blackish, with broad olive or yellowish lateral fringes, whitish tips	blackish, with yellowish-white lateral fringes, white tips
greater wing-coverts	blackish, broadly tipped olive	blackish, broadly tipped olive	blackish, tipped whitish or yellowish white, some with yellowish lateral fringes
median wing-coverts	broad olive tips	broad olive tips	tipped whitish, beige or olive-beige
wing chord	66–71 (69) $n = 11$	69–73 (71) $n = 7$	67–72 (69) $n = 15$
bill length (nostril to tip)	8.5–9.5 (9.1) $n = 11$	8.1–9.0 (8.4) $n = 7$	7.9–9.3 (8.5) $n = 15$
bill depth	5.4–6.1 (5.8) $n = 9$	5.8–6.1 (6) $n = 5$	5.7–6.4 (6.1) $n = 12$

but the streaking is sometimes broader, softer and / or greyer, and some examples of the streaked morph have underparts approaching typical grey-morph birds (Fig. 2g). Thus, although the grey morph does not seem intermediate between streaked and olive morphs, there is some approach between streaked and grey morphs, as well as between grey and olive morphs. The belly is yellow in adults of the olive morph and white in adults of both the grey and streaked morphs. The cap of grey birds is variable, being either not black like streaked birds, or black like olive birds, though rarely is it as black and as well defined. Thus cap coloration of grey birds exhibits a range of intermediate states. The wing-coverts of grey and olive birds are similar, with very broad olive tips. The wing-coverts of streaked birds are quite variable, often with narrow pale tips. However, these markings may be darker or more olive, and thus somewhat similar to, but still distinct from, the broad olive tips to the coverts of olive-morph and grey-morph birds. Table 2 presents a summary of plumage characters in the *S. pinus* / *S. atriceps* complex.

Our results confirm van Rossem's (1938) suggestion that olive-morph birds are distinguished by their longer and more slender bills (Fig. 5, Table 2), but we found no significant difference between the bills of streaked-morph and grey-morph birds. Our sample may fail to present a complete representation of each morphotype's geographic distribution, but we note that a series of 25 birds collected in central Chiapas includes three grey individuals and no olive birds (Fig. 1). Thus putative 'hybrids' are present where one of the 'parent' species may be absent. Grey morphs do not appear to present an intermediate

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character state between the olive and streaked morphs. However, *S. p. perplexus* displays a range of characters intermediate between grey-morph birds and *S. p. macropterus*.

Polymorphism might also be considered, with grey birds representing a morph of either *S. pinus perplexus* or *S. atriceps*. Plumage polymorphism is evident in other carduelines (e.g. in Lesser Goldfinch *S. psaltria*, and in females and immatures of Andean *S. spinescens* and Hooded Siskins *S. magellanicus*: DD pers. obs.).

Recent genetic studies have revealed that the grey and streaked forms are closely related, and together form a separate lineage from the olive form (Mila *et al.* in prep.). Although neither syntype was sampled by that study, these results suggest that the grey and olive syntypes of *S. atriceps* may be representatives of different taxa. We recognise that van Rossem's use (1938: 135) of the phrase 'the type' in reference to a specimen that is demonstrably the olive syntype (BMNH 1885.12.14.1179) constitutes designation of an *S. atriceps* lectotype. Fig. 3a shows that BMNH 1885.12.14.1179 bears a red type label, and this specimen was listed in Warren & Harrison (1971) as a syntype. These authors added that the second syntype is also at BMNH, but they rarely listed lectotypes. While grey birds have lingered in nomenclatural confusion, olive-plumaged birds have always been associated with the name *atriceps* and this is reflected in many popular and systematic treatments (Ridgway 1901, van Rossem 1938, Blake 1953, Miller *et al.* 1957, Alvarez del Toro 1971, Davis 1972, Peterson & Chalif 1973, Land 1970, Howell & Webb 1995, Clement 2010). This designation maintains applicability of existing nomenclature and stability of usage. Against this, van Rossem's (1938) designation may yield the result that, should the olive and grey morphotypes prove not to be conspecific, Salvin's (1863) diagnosis of *atriceps* would present characters of a form that differs from modern interpretations of that taxon.

Conclusions

Species limits in the *S. atriceps* / *S. pinus* complex remain poorly understood, and many authorities have followed van Rossem (1938) in suggesting that these forms hybridise and may be conspecific (e.g. Howell *et al.* 1968, AOU 1983, Sibley & Monroe 1990, Howell & Webb 1995, Clement 1993, 2010). The collection of additional vouchered, genetic material from the Chiapas and Guatemalan highlands is required to shed further light on the nature of plumage variation, species limits and perhaps phylogenetic relationships in the *S. pinus* / *S. atriceps* complex. Sound-recordings of vouchered specimens might also provide valuable data. Sampling, assembly and analysis of genetic data, together with data from the syntypes of *S. atriceps* and holotype of *S. pinus perplexus*, offer the best promise of lasting resolution.

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APPENDIX 1: Specimens examined.

Olive morphotype: AMNH 397802–808; USNM 349770–771; UMMZ 110328–329; WFVZ 14540–543, 14548. From photographs: BMNH 1885.12.14.1179, 1899.2.1.575–580; KU 111825.

Grey morphotype: DMNH 34695–696; LSUMZ 49577; MLZ 57023; USNM 143723–725. From photographs: BMNH 1885.12.14.1180, 1899.2.1.581–584, 1899.2.1.587.

Streaked morphotype: DMNH 27315–318; LSUMZ 49581–582; MLZ 50012–014, 56848, 56892, 57018, 57024; USNM 194298–299; UMMZ 109557; WFVZ 3449, 3165, 11326. From photographs: BMNH 1899.2.1.2115–2116, 1899.2.1.585–586, 1899.2.1.588, 1899.2.1.844.

Unidentified juveniles: USNM 143748–750. From photographs: BMNNH 1899.2.1.845.

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